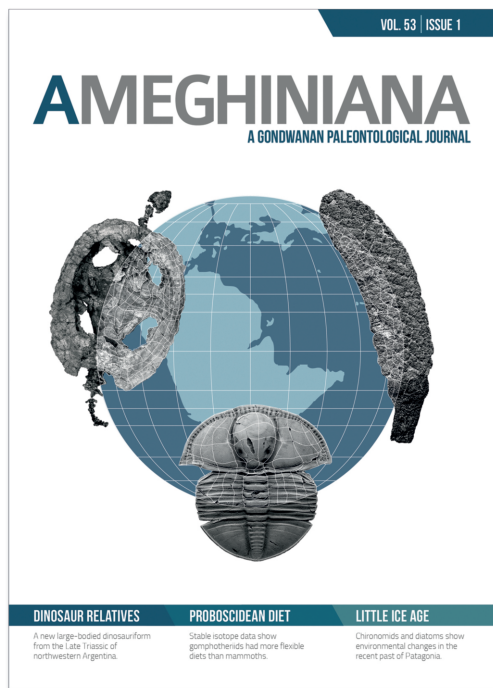




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ISOLATED LITOPTERNA POSTCRANIAL REMAINS FROM LA BARDA TUFF (EARLY EOCENE), PASO DEL SAPO, CHUBUT, ARGENTINA: PROPOSED ASSOCIATION WITH DENTAL TAXA AND THEIR IMPLICATIONS

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Abstract. The fossil remains from La Barda locality are part of the Paso del Sapo fauna (Chubut, Argentina), the main early Eocene mammal assemblage from west-central Patagonia. Until now, mammals from La Barda had only been recognized by isolated teeth and osteoderms. In this study, postcranial Litopterna remains were identified and segregated into morphological groups, or morphotypes, and their sizes were correlated with litoptern teeth. Morphotype 1 is represented by one astragalus similar to those of post-Deseadan litopterns. Morphotype 2 groups more generalized tibiae, astragali and calcanei which are similar to basal Protolipternidae (e.g., *Miguelsoria*). The regression model was derived from a known sample of 62 extant and fossil mammals. A 99.7% confidence interval was used to accept or reject a possible relationship between postcranial and dental remains. Dental remains from La Barda have been referred to two species of *Asmithwoodwardia* (Protolipternidae?). The dental size of both species correlates well with morphotype 2. However, the largest, more derived morphotype 1 astragalus does not appear to be represented in the fauna by any dental remains. This brings to the table the importance of postcranial remains to the comprehension of the diversity of ancient faunas.

Key words. Litopterna. Eocene. Astragalus. Morphotypes. Didolodontidae.

Resumen. RESTOS POSTCRANEANOS AISLADOS DE LA TOBA LA BARDA (EOCENO TEMPRANO), PASO DEL SAPO, CHUBUT, ARGENTINA. Los restos fósiles de la localidad de la Barda pertenecen a la fauna de Paso del Sapo (Chubut, Argentina), la principal asociación de mamíferos fósiles del Eoceno temprano del centro oeste patagónico. Hasta ahora, los mamíferos de La Barda han sido reconocidos solamente por dientes aislados y osteoderms. Aquí, restos postcraneanos aislados de Litopterna fueron identificados y separados en grupos morfológicos o morfotipos, y su tamaño fue contrastado con el de dientes de litopternas. El morfotipo 1 está representado por un astrágalo similar al de los litopternas post-deseadenses. El morfotipo 2 agrupa tibias, astrágalos y calcáneos más generalizados y es similar a los Protolipternidae basales (e.g., *Miguelsoria*). El modelo estadístico está basado en una muestra de 62 mamíferos actuales y fósiles. Un intervalo de confianza del 99.7% fue usado para aceptar o rechazar una posible relación entre restos postcraneanos y dentarios. Dos especies de *Asmithwoodwardia* (Protolipternidae?) fueron identificadas mediante dientes de La Barda. El tamaño dental de ambas muestra una buena correlación con el morfotipo 2. Sin embargo, el más derivado morfotipo 1, de tamaño mayor, no parece estar representado en la fauna por ningún resto dental. Esto demuestra la importancia de los restos postcraneanos en la comprensión de la diversidad de faunas antiguas.

Palabras clave. Litopterna. Eoceno. Astragalo. Morfotipos. Didolodontidae.

TEETH are generally considered the most representative and the better preserved remains of ancient mammalian faunas. As they cannot always be related to other bones of the same localities, a large number of isolated postcranial elements remain unstudied in paleontological collections. However, some eutherian taxa are recognized by synapomorphies that appear in systems other than the digestive or the neurocraneal. Because different systems can evolve at different rates producing what it is called "mosaic evolu-

tion" (Gould, 1977; Mayr, 2001), data from different parts of the body are equally important to understand animals and their history. For example, the first representatives of Cetartiodactyla show a bunodont dentition similar to those of Hyposodontidae archaic ungulates, but the tarsus already shows a double-pulley astragalus, a synapomorphy of the clade (Simpson, 1937; Schaeffer, 1947; Geisler *et al.*, 2007). In that context, the study of postcranial remains should be as tenacious as those of craneodental traits, but partial or

complete Paleocene-Eocene skeletons are rare. The Paleocene-Eocene localities in South America generally lack complete or even partial articulated skeletons. Most postcranial remains are isolated, often broken and incomplete, most of the time found in a chaotic mix including remains of several taxa, which complicates their assignation to species, most of which are defined only by their dentition. Paleocene-Eocene mammals are usually basal species key to interpret morphological characters and reconstruct the phylogenetic relationships within Mammalia.

Ameghino was the first to assign to native South American ungulate species remains other than teeth, focusing particularly in astragali. But he did not provide any argument for the associations made by him, with one exception: *Notostylops*. Shockey and Flynn (2007) hypothesized that many of Ameghino's assignations were made in fact by his brother Carlos in the field, where he had more complete skeletons. For some of the localities where Carlos Ameghino worked this is very unlikely as they often lack articulated bones. Although several assignations of Ameghino were confirmed later based on more complete skeletons (e.g., *Nesodon*, *Adinotherium*, *Rhynchippus*, *Trachytherus*; see Shockey and Flynn, 2007), as Simpson concluded in his work of 1967 (p.193–194) some are not to be trusted: for example, Ameghino assigned tarsal remains of Hystricomorpha rodents to the notoungulates *Pachyrucos typicus* (Ameghino, 1904: fig. 65) and *Oldfieldthomasia septa* (Ameghino, 1905; fig. 52) and to the metatherian *Eodidelphys fortis* (Ameghino, 1905; fig. 10). These incorrect assignations probably were more related to the ideas that Ameghino had about the evolution of mammals than to a lack of anatomical knowledge.

Faunal Assemblage

Paso del Sapo Fauna is one of the most diverse late early Eocene mammalian faunas of Patagonia (Tejedor *et al.*, 2009). Considered first as early Eocene (Tejedor *et al.*, 2009), later it was dated as late early Eocene (Woodburne *et al.*, 2014), filling a temporal gap between Riochican (early Eocene) and Casamayoran (middle Eocene) South America Land Mammal Ages. The so-called Sapoan fauna comprises fossil remains of several metatherians ("Didelphimorphia", Paucituberculata, Sparassodonta, Microbiotheria and Polydolopimorphia) and eutherian mammals (Xenarthra, Chiroptera, archaic Didolodontidae ungulates, and South

American native ungulates: Litopterna, Notoungulata and Astrapotheria), all of them recognized based upon dental remains, or in the special case of xenarthrans by their osteoderms (Tejedor *et al.*, 2009).

The Sapoan fauna is represented at two localities, Laguna Fría and La Barda, located in northwestern Chubut Province, Argentina, near the town of Paso del Sapo, along the middle course of the Chubut River. Laguna Fría has more diverse dental remains representing more genera and families than at La Barda. But at La Barda fossil remains are more abundant and better preserved. La Barda is exceptional as nearly two thousand remains have been recorded, of which craneo-dental remains of ungulates are less than 10% (N=144). The most abundant bones of ungulates are phalanges (N=856), followed by metapodials (N=189), vertebral bodies (N=113), astragali (N=98) and calcanei (N=97). Phalanges, metapodials and vertebral bodies are difficult to identify and have been traditionally less studied. Contrarily, astragali and calcanei have been better studied and have shown to carry diagnostic traits. They were separated by their morphological characters into several morphotypes (Lorente, 2015). Two astragalar morphotypes from La Barda were recognized as belonging to the ungulate order Litopterna.

Litopterna is the second most diverse order of South America native ungulates. They were not exclusive of South America, as litopterns have also been found in the Eocene of West Antarctica (Bond *et al.*, 2006; Gelfo *et al.*, 2015). They differ from other South American ungulate orders in the specialized appendicular morphology they acquired very early in their evolution, while their bunoselenodont teeth remained very similar to the bunodont dentition of the archaic ungulates Didolodontidae. A close relationship between both taxa, Litopterna and Didolodontidae, has been supported by several authors (Ameghino, 1903; Scott, 1913; Simpson, 1934; Cifelli, 1983a, 1983b, 1993; Soria, 2001; Gelfo, 2006), with the Didolodontidae even been proposed as litopterns in the revision of the order by Scott (1913). Some dentitions previously considered didolodontid were associated with litoptern-like tarsal remains (e.g., *Miguelsoria*, Cifelli, 1983b) and have been regrouped with litopterns in the new basal family Protolitopternidae. Protolitoptern tarsals are characterized by a variable combination of pleisomorphic and apomorphic characters, while the morphology of later litoptern families is less variable.

MATERIALS AND METHODS

This study is based upon postcranial remains from La Barda referred to the Litopterna (Lorente, 2015). These include two tibiae, five astragali and two calcanei, which are housed in the Colección de Paleovertebrados del Laboratorio de Investigaciones en Evolución y Biodiversidad, Facultad de Ciencias Naturales, Universidad Nacional de la Patagonia “San Juan Bosco” (LIEB-PV). These elements were compared to fossil remains from Museo de La Plata and the American Museum of Natural History, and also with published data drawn from other litoptern skeletons (Scott, 1910; Cifelli, 1983a; Soria, 2001) and with the archaic ungulates Kollpaniinae (Muizon *et al.*, 1998). Each appendicular element (*e.g.*, tibia) was separated into several morphological groups, or morphotypes, and later different elements (*e.g.*, tibia and astragali) were regrouped as belonging to the same species or at least, genus, based upon the “fit” when articulated in anatomical positions (*e.g.*, astragalus trochlea into cochlea of distal tibia). Herein are described two distinct litoptern morphotypes, referred to 1 and 2 here and MTaC1 and MM3 in Lorente (2015). Bones are described with their topological names at least initially in Latin and italicized following the Nomina Anatomica Veterinaria (I.C.V.G.A.N. 2005) along with their colloquial names. To describe the calcaneus, its orientation is considered as if sustentacular and fibular facets were always dorsal.

Several measurements were taken with a digital caliper for better comparison (Table 1).

To test the assignation of some of these morphotypes to *Asmithwoodwardia* sp., a statistical generalized linear model was performed, with iteratively reweighted least squares (IRLS) optimization. The relationship of astragalar length as a function of m1 trigonid width, derived from a sample of 62 extant and fossil mammals from Lorente (2015) is given as follows:

$$\ln(\text{astragalar length}) = 1.06 \times \ln(\text{m1 trigonid width}) + 1.16$$

Using the leave-one-out cross validation method (using the statistical software R, R Core Team, 2014), a percent prediction error (PE%; Van Valkenburgh, 1990) was obtained with a standard deviation of 8.39%. A 99.7% confidence interval was used to accept or reject a possible relationship between dental and postcranial remains. This interval was established as the overall kurtosis of the comparison sample was low. Also, skeletons (N=4) from the literature (Scott, 1910) and from the MLP museum (N=1) were used as a control sample, with an error margin within -0.06 and -8.97 (Table 2).

Previous works have tried to associate isolated postcranial bones to dentally recognized species for the localities of Itaboraí, Brazil (early Eocene; Cifelli, 1983a; Bergqvist,

TABLE 1 – Values of La Barda dental and tarsal remains.

Genus/Family	Specimen	Trim1	Predicted value	PE% (LIEB-PV 4008)	PE% (LIEB-PV 4009)
Asmithwoodwardia subtrigona	LIEB-PV 1614	2.75	2.23	17.19	-0.15
	LIEB-PV 5082	3.34	2.44	7.28	-8.59
Amilnewardsiidae	LIEB-PV 1616	3.46	2.48	5.66	-9.97
Sparnotheriodontidae	LIEB-PV 1614	7.31	3.27	-19.97	-31.81
Morph	specimen	LA	Observed value (ln(LA))		
1	LIEB-PV 4008	13,68	2.62		
2	LIEB-PV 4009	9.29	2.23		

Measurements in mm. LA: astragalar length; PE%: Percentual Prediction Error; Trim1: first inferior molar trigonid width; Predicted value for formula $\ln(\text{astragalar length}) = 1.06 \times \ln(\text{m1 trigonid width}) + 1.16$.

TABLE 2 – Values of *Litopterna* with known skeletons.

Genus/Family	Specimen	Trim1	LA	Predicted Value	PE%
<i>Diadiaphorus majusculus</i>	YPM-VPPU 15799*	13.5	44	3.92	-3.44
<i>Diadiaphorus majusculus</i>	AMNH 9291	14	39	3.96	-7.43
<i>Thoatherium minusculum</i>	YPM-VPPU 15719*	9	28.5	3.49	-3.99
<i>Theosodon gracilis</i>	YPM-VPPU 15798*	20.5	53	4.36	-8.97
<i>Macrauchenia</i> sp.	MLP 12-1424	21.3	81.4	4.40	-0.06

Measurements in mm. LA: astragalar length; PE%: Percentual Prediction Error; Trim1: first inferior molar trigonid width; Predicted value for formula $\ln(\text{astragalar length}) = 1.06 \times \ln(\text{m1 trigonid width}) + 1.16$. *Scott, 1910.

1996, 2008), and of early Paleocene of Tiupampa, Bolivia (Muizon *et al.*, 1998). These works used four different criteria for the assignation: morphology, relative size, abundance and “fit”. “Fit” and morphology are considered and discussed in this work (see below). Relative abundance seems not a valuable criterion for La Barda materials, as the postcrania of larger animals are more abundant than of smaller taxa and the opposite seems to be true for teeth, as the smaller species are far more abundant. Postcranial elements of metatheria, the more abundant group represented by teeth in La Barda but also comprising the smallest taxa, are almost inexistent; in turn the larger Notoungulata family Notostylopidae, represented by a dozen of incomplete teeth, is the second most abundant group in postcranial remains (Lorente, 2015). The collection method cannot be blamed for this difference in preservation as La Barda was subject of intense screen washing. Relative size was, as here, compared with regression models, but previous models show several problems when applied elsewhere. For further discussion of linear regression models and applications in previous works see Gelfo and Lorente (2012) and Lorente (2015).

Institutional abbreviations: LIEB-PV, Colección de Paleovertebrados del Laboratorio de Investigaciones en Evolución y Biodiversidad, Facultad de Ciencias Naturales, Universidad Nacional de la Patagonia “San Juan Bosco”, Esquel, Chubut, Argentina; MLP, División Paleontología de Vertebrados, Museo de la Plata, La Plata, Buenos Aires, Argentina; UF, Florida Museum of Natural History, Florida, USA; YPM-

VPPU, Yale Peabody Museum, Vertebrate Paleontology Princeton University Collection, New Haven, USA.

RESULTS

The astragali here analyzed were identified as litopterns because they have a deep trochlea, with long, parallel trochlear crests, with the lateral crest larger and higher than the medial one; a laminar navicular facet (which means that the facet extends dorsoplantarily but not at the sides; Lorente, 2015); a lateral (or fibular) facet that covers the lateral process, which indicates that the calcaneus most probably had a fibular facet too; a C-shaped medial malleolar facet, restricted to the crest; and sustentacular facet extending in most of the anteroposterior axis.

Morphotype 1

Figure 1

It includes only one left astragalus (LIEB-PV 4008). It is particularly eroded for the locality, where bones, although broken, have in general a remarkable state of conservation with observable muscular insertions and origins. It has several postmortem cavities with sharp borders. The ectal facet is complex, markedly concave and C-shaped, reaching far beyond the lateral crest in dorsal view. The lateral process is projected, and covered by the fibular facet. The trochlea has an anterior facet for the articulation with the tibia. The plantar extension of the navicular facet reaches half of the sustentacular facet. The sustentacular facet is round in its posterior half and enlarges towards the anterior end. There

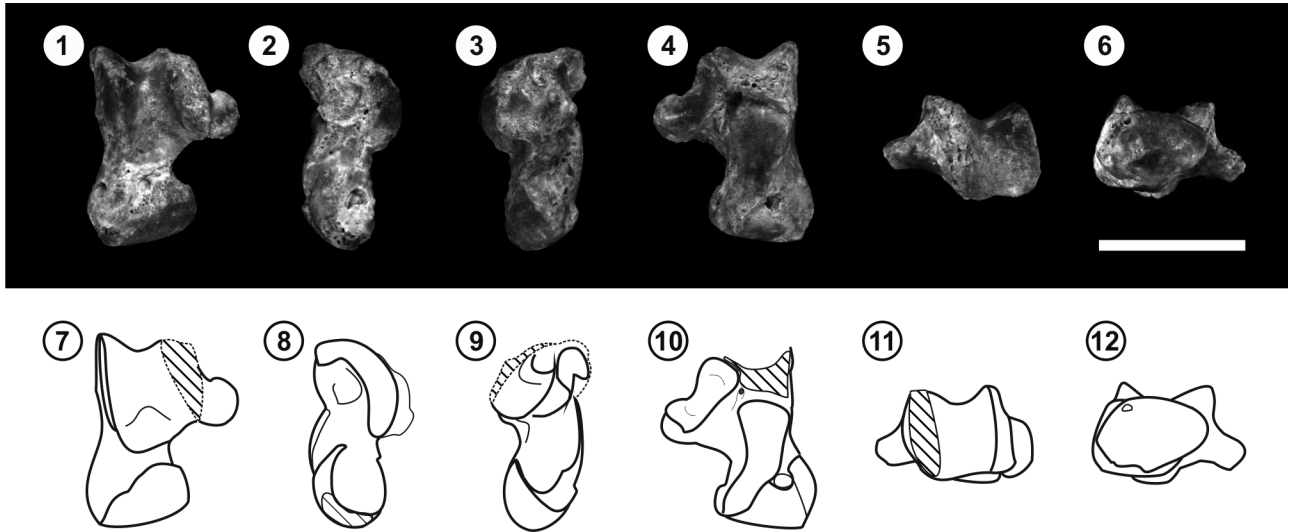


Figure 1. Morph 1, astragalus LIEB-PV 4008. Views: 1-7, dorsal; 2-8, medial; 3-9, lateral; 4-10, plantar; 5-11, posterior (proximal); 6-12, anterior (distal). Scale bar= 10mm.

is no astragalus foramen or fossa in the posterior surface of the trochlea. It presents several foramina between the trochlear anterior facet and the navicular facet, between the navicular facet and the sustentacular facet, and between the navicular facet and the plantar extension of the navicular facet. The navicular facet and its so-called “plantar extension”, although fused, are quite clearly distinct facets in Litopterna. In archaic ungulates there is a medial extension of the navicular facet that has been called the “facet for the medial collateral ligaments” by Cifelli (1983a: p. 3; fig. 1). It is preferred here to call it “extension of the navicular facet” because, at least in Notoungulata, this facet articulates with the navicular, and is not for the collateral ligaments. In Litopterna, this extension is more plantar and, although fused with the navicular facet, it does not articulate with the navicular. The litoptern navicular has an extra plantar facet than, when articulated with the astragalus, forms a single oval facet with this extension. It is currently not known what this peculiar facet between the bones is for (perhaps ligaments or a sesamoid).

The foramina of the astragalus, together with the erosion of the bone, may indicate that it belonged to a juvenile animal (personal observation). Astragalus develops from a single ossification center and there is no current objective criterion to differentiate juvenile from adult astragali, but it has been observed that some astragali from actual juvenile

mammals show foramina not present in adult specimens (e.g., MLP 28.VIII.98.2 *Ozotoceros bezoarticus*). However, a proper study about this subject is still pending, and this criterion should be taken cautiously. This astragalus measures 13.68 mm in length and has an error when associated with *Asmithwoodwardia* lying within 7.28% and 17.19% (Table 1). This error is within the 99.7% established margin, being the larger error next to the second standard deviation, but it is of positive sign, while known litopterns tested with this model have a consistent negative error.

Morphotype 2

Figures 2–4

It groups two tibiae, four well preserved astragali and two calcanei. Tibiae and calcanei have been associated with these astragali because they “fit”, which means that they articulate correctly.

Tibiae. (LIEB-PV 4703; LIEB-PV 4704; Fig. 2) two left distal tibial epiphysis. Their transversal shape is quadrangular. The dorsolateral border forms a crest interrupted before the distal end. They have a triangular shaped *malleolus medialis* (medial malleolus). There is no *malleolaris sulcus*. The cochlea presents a deep medial fossa and an oblique lateral facet for the articulation with the astragalus. The lateral facet is bordered by a thin fibular facet. There is no dorsal facet in

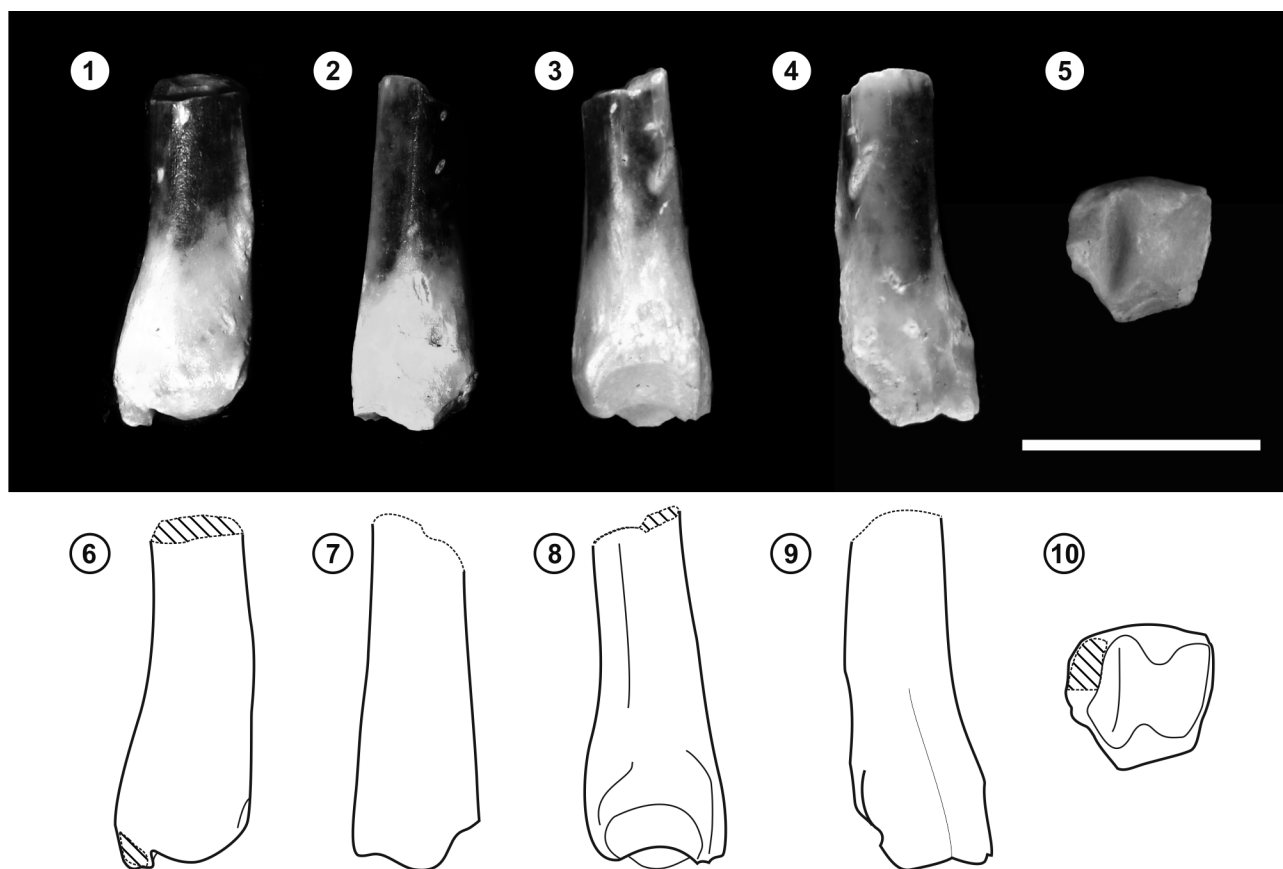


Figure 2. Morph 2: tibia LIEB-PV 4703. Views: 1-6, dorsal; 2-7, medial; 3-8, lateral; 4-9, plantar; 5-10, distal. Scale bar= 10mm.

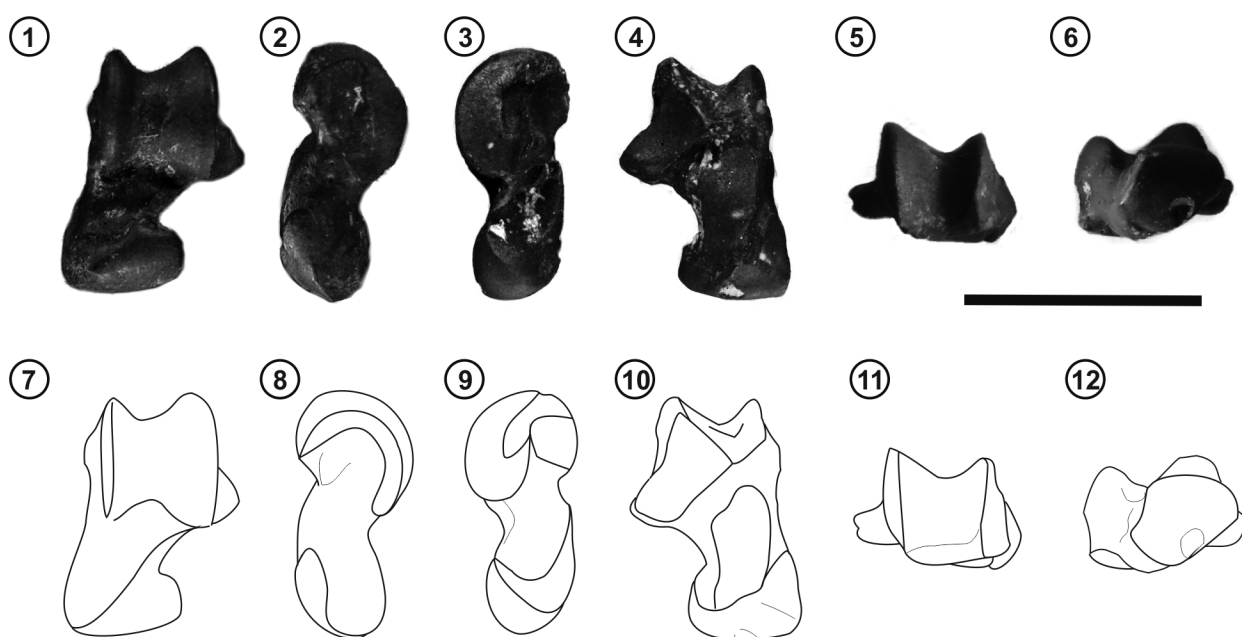


Figure 3. Morph 2: astragalus LIEB-PV 4009. Views: 1-7, dorsal; 2-8, medial; 3-9, lateral; 4-10, plantar; 5-11, proximal; 6-12, distal. Scale bar= 10mm.



Figure 4. Morph 2: calcaneus LIEB-PV 4107. Views: 1-5, dorsal; 2-6, medial; 3-7, lateral; 4-8, plantar. Scale bar= 10mm.

the dorsodistal border of the epiphysis, which is characteristic of the better known litoptern families (e.g. Proterotheriidae *Megadolodus*, *Proterotherium*, Macraucheniidae *Theosodon*, *Macrauchenia*; Lorente, 2015). The presence of a developed medial malleolus indicates a probable assignation of these bones to Protolipternidae.

Astragali. (LIEB-PV 4009; LIEB-PV 4010; LIEB-PV 4012; LIEB-PV 4013; Fig. 3): four left astragali, one complete (LIEB-PV 4009) and three trochleas, smaller than LIEB-PV 4008. They possess a small *flexor sulcus* (flexor groove), observable under the magnifier but difficult to distinguish with naked eye. The ectal facet is simple, deeply concave, with a

triangular shape and less projected than in LIEB-PV 4008. There is a small astragalar medioplantar tubercle. A dorsal nuchal crest in LIEB-PV 4009 runs from the navicular facet to the trochlea. The length of LIEB-PV 4009 is 9.29 mm, with percent errors for the statistical model when associated with *Asmithwoodwardia* within -0.15% and -8.57% (Table 1), similar to the errors for other litopterns.

Calcanei. (LIEB-PV 4107; LIEB-PV 4184; Fig. 4) one right and one left elongated calcanei. They have a small, concave, inverse drop-like sustentacular facet; a convex and slightly extending to the tubercle facet; a convex fibular facet, half the size of the ectal one, and a concave, very oblique, cuboid

facet. There is a sagittal crest between ectal and sustentacular facet, typical of litopterns (but also present in some rodents; Lorente, 2015). Below the ectal prominence, there is a rectangular non articular surface, part of the peroneal process. The ectal prominence is small, dorsally projected. The calcaneal body is straight and has no “beak” (characteristic of notoungulates and some archaic ungulates, Cifelli, 1983a). The plantar tubercle is thin and more anterior than the peroneal process. The tuber presents a lateral fossa.

DISCUSSION

In general, morphotype 2 is more primitive than morphotype 1, similar to the bones associated to the Protolipternidae *Miguelsoria* and *Protolipterna* (Cifelli, 1983a; Bergqvist, 1996). In contrast, morphotype 1 is more similar to Protherotheriidae and Macraucheniidae and therefore more derived.

Morphotype 2 and Protolipternidae have several characters absent in the better known litoptern families Protherotheriidae and Macraucheniidae, as follows:

1-Presence of a well developed medial malleolus in the tibia. Later litopterns have a very reduced or absent medial malleolus.

2-Absence of a dorsal distal facet in the tibia and, in correspondence, absence of an anterior trochlear facet in the astragalus.

3-A simple triangular ectal facet both in the astragalus and in the calcaneus. Protherotheriidae and Macraucheniidae have a complex heart-shaped ectal facet.

4-Invert drop-like sustentacular facet in the calcaneus, similar to that of notoungulates; later litopterns have a kidney-shaped sustentacular facet.

5-Dorsal nuchal crest in the astragalus extending from the head to the trochlea. Protherotheriidae and Macraucheniidae lack one. It is also present in the astragalus assigned to the Kollpaniinae *Tiuclaenus* (Muizon *et al.*, 1998) and in the Protolipternidae *Miguelsoria* (Bergqvist, 1996, p. 165).

In this sense, postcrania assigned to Protolipternidae fit with the description by Simpson (1948, p. 96) of Didolodontidae astragali: “*They most closely resemble the astragali of Litopterna among other orders, but lack litoptern specializations*”. However, Simpson did not describe what specializations didolodontid astragali lack. But to be less specialized

(more generalized) than these Protolipternidae and to resemble more closely North American archaic ungulates or Notoungulata (which has a more generalized appendicular morphology, particularly in basal forms), didolodontid astragali should have a shallower trochlea, a flexor groove (which Simpson indicates that didolodontids lack), and/or a more spherical head. This description fits closely to the astragalus assigned to the kollpaniinae *Tiuclaenus* from the early Paleocene of Tiupampa, Bolivia (Muizon *et al.*, 1998). The astragalus assigned to *Tiuclaenus* also lacks the characteristic semispherical head of other archaic ungulates, and has a more constricted laminar one (see above), with the navicular facet extending dorsoventrally as in litopterns. Even more, a litoptern-like astragalus has been recorded from the locality of Laguna Fría; it has a well developed flexor groove, being more “primitive” than those described by Simpson (1948). The better candidates by size for the Laguna Fría astragalus are two species of didolodontids represented at this locality but not found in La Barda (Lorente, 2015).

Cifelli (1983a) and Bergqvist (1996, 2008) proposed a completely different set of features for the postcranium of Didolodontidae, assigning to this family bones that were considered to resemble more closely those of archaic ungulates (“condylarths”). There are several differences between the postcranium assigned to Itaborai didolodontids and those of North American archaic ungulates, and also to the extensive description by Simpson (1948) (see Table 3). Other authors have proposed that this postcranium could be assigned to other orders, probably Notoungulata (Soria, 2001; Lorente, 2015) or Astrapotheria (Lorente, 2015). As an example, the astragali assigned to *Victorlemoinea* (Cifelli, 1983a) or to *Condylarthra* indet. (Bergqvist, 1996) has a well developed latero-plantar cuboid facet, a feature that among South American native ungulates is only known in the order Astrapotheria.

Scott (1913) was the first to consider didolodontids as a family within Litopterna (Didolodidae [sic]), although he proposed a rather primitive hypothetical skeleton for them. Before that, Ameghino (1905) assigned two litoptern-like astragali to *Asmithwoodwardia subtrigona* and *Lambdaconus porcus*. He considered *Asmithwoodwardia* not as a litoptern, but as one of the most primitive condylarths and *Lambdaconus* as an antecessor of *Didolodus* (Ameghino, 1905). He

TABLE 3 – Comparison between Simpson (1948) didolodontid astragali description and other Astragali.

Simpson (1948)	AMNH 117457	AMNHFn443	Morphotype 1	Morphotype 2	Laguna Fria	Thoatherium	Tiucuaenus?	Phenacodus
Throclea: broad and well excavated	broad and shallow	Long and shallow	broad and well excavated	broad and well excavated	broad and well excavated	long and well excavated	broad and shallow	broad and well excavated
Fibular crest more elevated	Crests of a similar height	Fibular crest more elevated	? (fibular crest broken)	Fibular crest more elevated	Fibular crest more elevated	Fibular crest more elevated	Crests of a similar height	Fibular crest more elevated
Bottom of the throclea on the tibial side	Equidistant	Bottom of the throclea on the tibial side	Bottom of the throclea on the tibial side?	Bottom of the throclea on the tibial side	Bottom of the throclea on the tibial side	Bottom of the throclea on the tibial side	Equidistant	Bottom of the throclea on the tibial side
Both crest fairly sharp	Rounded crests	Rounded crests	Sharp crests	Sharp crests	Sharp crests	Sharp crests	Sharp fibular crest, rounded tibial crest	Sharp fibular crest, rounded tibial crest
Internal tibial facet small	Very developed facet with cotylar fossa	Very developed facet with cotylar fossa	Restricted to the crest (small)	Restricted to the crest (small)	Restricted to the crest (small)	Restricted to the crest (small)	Restricted to the crest (small)	Restricted to the crest (small)
Neck oblique, rather short, somewhat constricted	oblique, well developed and wide	oblique, well developed and wide	Oblique, long and constricted	Oblique, long and constricted	? (broken)	Oblique, short and constricted	Oblique, long and constricted	Oblique, short and constricted
Head somehow flattened dorsoventrally and with convex navicular facet	Well developed, particularly wide transversally	Well developed, particularly wide transversally, almost subspherical	laminar (developing dorsoventrally but not at the sides), convex	Laminar and convex	? (broken)	Laminar and convex	Laminar, somehow flattened	Semispheric
No internal projection, but a Phenacodus like external projection	Both projection present but reduced	Both projection present but reduced	No internal projection, and a developed external projection	Internal projection reduced, and a developed external projection	Internal projection reduced, and a developed external projection	Internal projection reduced, and no external projection	Both well developed	No internal projection, and a developed external projection
No foramen and no extension of the trochlear groove	Both present	Both present	Both absent	No foramen, trochlear groove very reduced	No foramen but well developed trochlear groove	Both absent	Both present	Both present
Sustentacular facet short	? (broken)	? (broken)	long	long	?	long	rounded	rounded
Ectal facet relatively wide, oblique, and deeply concave	Narrow, oblique? and flattened	Narrow, oblique? and flattened	Narrow, oblique and concave	Wide, oblique and concave	Wide, oblique and concave	Heart shaped, oblique, concave, complex and almost lateral	long, oblique and concave	long, oblique and concave

recognized their morphology as being similar to that of litopterns, particularly Proterotheriidae.

Later, Simpson (1948) performed an extensive description of isolated astragali he considered as belonging to Didolodontidae, as they appear in the same strata as didolodontid teeth in about the same proportions. Simpson did not illustrate them, as he intended to publish more extensive description. These astragali are currently lost, and which specimens in the AMHN they could be is subject to speculation. At least two specimens have been proposed as *Didolodus*, (AMNH 117457, AMNHF443) although they do not fit Simpson's (1948) original description (see Table 3).

Cifelli (1983a) was the first to explicitly propose that Litopterna evolved first postcranial adaptations, and later dental ones, and change the assignment of didolodontid genera with assigned litopterna postcrania to the new litoptern family Protolipternidae. Soria (2001) recognized the litopterna-like astragali assigned to Protolipternidae, but he rejected those non-litoptern-like tarsals assigned to Didolodontidae and to Sparnotheriodontidae. Soria went a step further proposing that all didolodontids should have had litoptern-like tarsals and, if this was true, it would be possible to classify all Didolodontidae as Litopterna as proposed by Scott (1913), being Protolipternidae a junior synonym of Didolodontidae.

The only litoptern genus present in La Barda is the Protolipternidae? *Asmithwoodwardia*, with the species *A. subtrigona* and *A. sp. nov.* (Tejedor *et al.*, 2009). *A. subtrigona* is more abundant and diverse. *A. sp. nov.* is within the size range of *A. subtrigona*.

Asmithwoodwardia has been traditionally considered as a Didolodontidae (Simpson, 1934, 1948, 1967; Soria and Hoffstetter, 1983; Hoffstetter and Soria, 1986; McKenna and Bell, 1997; Soria, 2001; Gelfo, 2006). It was previously classified as a Phenacodontidae by Ameghino (1906) and considered a Hyopsodontidae by Paula Couto (1952). It was removed from Didolodontidae and classified under Litopterna with doubts by Cifelli (1983b), because of the absence of hypocone in the third superior molar of *Asmithwoodwardia scotti* from São José de Itaboraí, Brazil. Gelfo and Tejedor (2004) and Gelfo (2006) continued considering *Asmithwoodwardia* as a Didolodontidae, as the species of Patagonia have an hypocone in the M3, and proposed that *A. scotti* should be removed into another genus.

Ameghino (1905) described an astragalus for *Asmithwoodwardia subtrigona* but he did not publish the arguments for this assignment, and it must be considered cautiously. This astragalus is remarkably similar to the Morph 2 astragali in general morphology, although some differences can be observed. The astragalus figured by Ameghino seems to have an anterior trochlear facet and to lack a nuchal crest (Ameghino, 1905: fig. 20), but none of these characters are described in the text (the specimen is currently lost). It has to be noted that the neck of Morph 2 forms a concavity next to the trochlea, which is remarkably similar to the anterior trochlear facet of later litoptern families, but has no borders, and after cleaning and whitening of the bone with ammonium chloride (Feldmann, 1989), it is clear that it does not constitute an articulation surface.

With a Protolipternidae morphology and smaller percent errors with a negative sign, Morph 2 is assigned to *Asmithwoodwardia* sp. as it is possible that different species of the same genus have the same postcranial morphology, especially if they share a similar size.

Morph 1 has a more derived morphology, similar although not identical with the first astragalar remains of the Proterotheriidae *Protheosodon* (Loomis, 1914; Amherst Collection 3001) and the Macraucheniidae *Coniopternium* (Shockey, 1999; UF 172424 and UF 172426) from the De-seadean (late Oligocene). The Proterotheriidae *Protheosodon* was found near a *Protheosodon* jaw but it is not possible to assess if they belong to the same individual. Even though, it has several features present in Litopterna, *i.e.*, 1) reduction of the tibial malleolus, 2) dorsal facet in the distal epiphysis of the tibia, 3) deep trochlea with sharp crests in the astragalus, 4) laminar astragalar head, 5) astragalar anterior trochlear facet, 6) reverse alternating tarsus (which has been described for Notoungulata by Cifelli, 1993, but it is quite common in Litopterna as well; *e.g.*, *Theosodon*, *Macrauchenia*, *Proterotherium*).

The families Macraucheniidae, Proterotheriidae and Adiantidae were grouped in Lopholipterna by Cifelli (1983b) and later supported by Soria (2001). Morph 1 is smaller and more slender than the Oligocene genera, with a narrower and longer neck. But the greatest difference between Morph 1 and the Oligocene genera seems to be the presence in the later of a very complex ectal facet, convex at the extremes and very concave in the middle. Taking into account the al-

most twenty million years gap between Sapoan Fauna and the Deseadean, this seems like a very small difference and this astragalus could have belonged to the most ancient lopholiptern known to the date.

There is no other litoptern or didolodontid recognized by teeth in La Barda. In Laguna Fría, where *Asmithwoodwardia subtrigona* is also present, there are also two other litoptern families: Amilnedwardsiidae and Sparnotheriodontidae. Species present in Laguna Fría could have been in La Barda, and vice-versa. An association between Amilnedwardsiidae molar teeth and Morph 1 is rejected, as the representatives of these families are similar in the size to *Asmithwoodwardia*.

The Sparnotheriodontidae has been considered as Didolodontidae by Cifelli (1983a) and Bergqvist (1996, 2008) based on the association of several isolated postcranial remains, and that was used to justify removing Sparnotheriodontidae from the order Litopterna. Posterior authors have kept the family within Litopterna, with the argument that the dentition is too derived for Didolodontidae and the associations mentioned above too controversial (Wyss *et al.*, 1994; Soria, 2001; Gelfo, 2006; Lorente, 2015). The possible association of Morph 1 with Sparnotheriodontidae molars has a percent error near the confidence limit. The molars of this family found in Laguna Fría seem too large for this astragalus (PE%=-19.97). It could be that the astragalus belonged to a juvenile and had not reached its full size. But astragali of juvenile extant artiodactyls with similar conditions, particularly the presence of multiple foramina between different facets, have already reached lengths comparable to those of adults, although they are more slender. If Morph 1 belonged to a Spartheriodontidae, it would signify that this family showed an early derived morphology not only in their dentition but also in the appendicular skeleton, confirming the hypothesis of Soria (2001) that previous postcrania associated to this family were actually from another order (Soria, 2001, proposed that they were from an unknown Notoungulata, but recently the Astrapotheria *Tetragonostylops* has also been proposed; see Lorente, 2015), and that Spartheriodontidae did have a litoptern-like skeleton. Also, this would have implications in how we interpret the relationships of this family: if Sparnotheriodontidae had an appendicular skeleton more similar to Lopholipterna than to Protolipternidae, it could well be a

basal family of later more advanced litopterna instead of a taxon without descendants as proposed by Soria (2001). Soria grouped Sparnotheriodontidae and Anisolambdidae in the separated suborder Eolitopterna with the conviction that these two families were more related between each other than to Lopholipterna.

Even though, the percent error of this association is too near the confidence limit and because of this, it is here decided that Morph 1 should remain not associated until further remains of the Sapoan Fauna are eventually recovered. If this was not a Spartheriodontidae, an unknown genus of an indeterminate litoptern family wandered La Barda, of which no dental remains have been found yet.

CONCLUSION

Morphotype 2 is here tentatively assigned to *Asmithwoodwardia subtrigona* and *Asmithwoodwardia* sp. nov., supporting the Protolipternidae condition of the Patagonian species of this genus, but also questioning the hypothesis that there were “true” didolodontids with a non litoptern-like postcrania. As proposed by Soria (2001), the idea supported here is that Didolodontidae had postcranial remains not very different from those of litopterns.

Morphotype 1 is more specialized and more similar to post-deseadean litopterns. It belonged to a specimen whose dental remains have yet to be found, and it shows the importance of postcranial bones in the comprehension of ancient faunas.

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